



1 Effect of the 2022 summer drought across forest types 2 in Europe

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11 **Abstract**

12 Forests in Europe experienced record-breaking dry conditions during the 2022 summer.
13 The direction in which various forest types respond to climate extremes during their
14 growing season is contingent upon an array of internal and external factors. These factors
15 include the extent and severity of the extreme conditions and the tree ecophysiological
16 characteristics adapted to environmental cues, which exhibit significant regional
17 variations. In this study we aimed to: 1) quantify the extent and severity of the extreme
18 soil and atmospheric dryness in 2022 in comparison to two most extreme years in the
19 past (i.e., 2003, 2018), 2) quantify response of different forest types to atmospheric and
20 soil drought in terms of canopy browning and photosynthesis, and 3) relate the functional
21 characteristics of the forests to the emerging responses observed at the canopy level.
22 For this purpose, we used the ERA5-Land spatial meteorological dataset between 1970
23 to 2022 to identify conditions with extreme soil and atmospheric dryness. We used the
24 near-infrared reflectance of vegetation (NIRv) derived from the MOderate Resolution
25 Imaging Spectroradiometer (MODIS), and the OCO-2 solar induced fluorescence (SIF)
26 as an observational proxy for photosynthesis based on the SIF data product, to quantify
27 the response of forests at the canopy level.
28 In summer 2022, particularly southern regions of Europe experienced the most
29 pronounced atmospheric and soil dryness. As a result, the extremely dry conditions led
30 to an average 30% more widespread decline in SIF across forests compared to drought



31 in 2018, and 60% more widespread decline compared to drought in 2003. Although the
32 atmospheric and soil drought were more extensive and severe (indicated by a larger
33 observed max z-score) in 2018 compared to 2022, the negative impact on forests,
34 indicated by declined SIF, was significantly larger in 2022. Across different forest types,
35 the deciduous broad-leaved forests were most negatively affected by the extreme
36 conditions in 2022, but Evergreen Needle-Leaf Forests (ENF) distributed in northern
37 regions of Europe showed enhanced canopy greening and SIF signals as a benefit of
38 warming. Higher degree of canopy damage in 2022 in spite of less extreme conditions
39 compared to the previous extreme year points to a legacy effect on forest canopies, and
40 a declined forest resilience in response to more frequent drought events.

41

42 *Keywords: photosynthesis, soil drought, atmospheric drought, canopy browning, gross*
43 *primary production*

44 **Introduction**

45 The frequency and intensity of drought events have been increasing globally, and future
46 global warming will continue to increase the occurrence of such events (Seneviratne et
47 al. 2012; Röthlisberger and Papritz 2023). Particularly over the past two decades, over
48 many regions in Europe, there have been reports of widespread drought conditions, for
49 example during the summers of 2003, 2010 and 2018 (Bastos et al. 2020; Zhou et al.
50 2023). Such extreme conditions lead to widespread ecological disturbance (Müller and
51 Bahn 2022) and reduced capacity of forests for carbon uptake which diminishes their
52 potential for mitigating climate change (van der Woude et al. 2023). Additionally,
53 heatwave and prolonged drought periods stress vegetation and increase their
54 susceptibility to other biotic and abiotic stress factors, increase tree mortality and risk of
55 wildfire, lead to loss of biodiversity of plants and animals that live on the edge of their
56 temperature tolerance, and change phenology and plant development with cascading
57 effects on the functioning of the ecosystem (Seidl et al. 2017).

58 The spatial extent and severity of drought events vary, and the impacts depend on the
59 local ecological characteristics of the forests, species-specific temperature and moisture



60 threshold that limit tree functioning, and adaptation strategies and acclimation of trees to
61 more frequent and more intense extreme conditions (Gessler et al. 2020). For example,
62 comparing the 2003 and 2018 extreme years, the year 2018 was characterized by a
63 climatic dipole, featuring extremely hot and dry weather conditions north of the Alps but
64 comparably cool and moist conditions across large parts of the Mediterranean. Negative
65 drought impacts appeared to affect an area 1.5 times larger and to be significantly
66 stronger in summer 2018 compared to summer 2003 (Buras et al. 2020).

67 In 2022 Europe experienced its second hottest and driest year on record and the summer
68 of 2022 was the warmest summer ever recorded. Conditions in summer 2022 led to
69 record-breaking heatwave and drought events across many regions (Copernicus Climate
70 Change Service, 2023). Compound drought and heatwave conditions in 2022 caused
71 widespread crop damage, water shortages, and wildfires across Europe. The hardest-hit
72 areas were Iberian Peninsula, France, and Italy, where temperatures exceeded 2.5°C
73 above normal, and severe droughts persisted from May to August (Tripathy and Mishra
74 2023). The reduced soil moisture due to precipitation deficits and high temperatures,
75 contributed to the persistence and severity of drought, creating a positive feedback loop
76 where dry soils led to even drier conditions (Tripathy and Mishra 2023).

77 Drought and heatwaves have diverse negative impacts on the functioning of trees and
78 forests. The most immediate response is that rising air temperature and increased
79 dryness (in the soil or in the atmosphere) leads to changes in mesophyll and stomatal
80 conductance that affect carbon uptake (Marchin et al. 2021). Plants reduce stomatal
81 conductance under severe drought to reduce water stress at the expense of reduced
82 rates of photosynthesis (Oren et al., 1999). Drought also increases the chance of
83 hydraulic failure and leads to tree mortality (Choat et al. 2018). In addition, under rising
84 temperatures enzymatic activity of trees is reduced which also decreases the gross
85 primary productivity of the forest (Gourlez de la Motte et al. 2020). Elevated temperatures
86 can also increase rates of respiration from the soil and from the trees which leads to
87 reduced net capacity of forests for carbon uptake and reducing anthropogenic CO₂
88 emissions (van der Molen et al. 2011; Anjileli et al. 2021). Drought also limits movement
89 of nutrients in the soil water and decreases nutrient availability to trees which would affect
90 growth and productivity (Bauke et al. 2022).



91 Changes in plant water-use and nutrient cycling can trigger feedback loops that magnify
92 the effects of drought and heat stress. For instance, reduced plant cover can increase
93 soil temperatures and further accelerate water loss and increase plant water demand
94 (Haesen et al. 2023). On the other hand, increased atmospheric dryness or reduced soil
95 moisture levels increase stomatal closure which limits transpiration and leads to higher
96 leaf temperature that intensifies heat stress on plants (Drake et al. 2018). Reduced
97 transpiration and photosynthesis lead to increased surface temperature and CO₂
98 concentration in the atmosphere, both of which change local and regional climate patterns
99 and accelerate the frequency and intensity of extreme events (Humphrey et al. 2018).
100 These responses depend largely on forest type and species composition, which
101 combined with the properties of the extreme (in terms of extent and severity) complicates
102 our understanding of how drought influences the functionality of different forest
103 ecosystems (Gharun et al. 2020; Shekhar et al. 2023a). These feedback loops
104 underscore the critical need to evaluate the repercussions of climate extremes on
105 different forest types, which play a pivotal role in sequestering significant portions of
106 anthropogenic emissions from the atmosphere, under a drying climate. Our objectives in
107 this study are thus to 1) quantify the extent and severity of the extreme conditions in 2022
108 (in terms of soil and atmospheric dryness) and compare that to two past extreme years
109 (i.e., 2003, 2018), 2) quantify response of different forest types to drought in terms of
110 canopy browning and photosynthesis, and 3) relate the functional characteristics of the
111 forests to the emerging responses observed at the canopy level.

112 **Methods**

113 *Meteorological dataset*

114 We used Europe-wide (Longitude: 11°W - 32°E; Latitude: 35.8°N -72°N, approximate
115 area of 4.45 million km²) gridded datasets of daily total precipitation (Precip; mm), daily
116 mean air temperature (T_{air}; °C), daily mean relative humidity (RH; %) and daily mean soil
117 moisture (SM; m³m⁻³) of topsoil layer (0-7 cm depth), spanning from 2000-2022. We
118 obtained the Precip, T_{air} and RH datasets from the E-OBS v27.0e dataset (daily at



119 0.1°×0.1° resolution; Cornes et al., 2018; Klein et al., 2002), and SM was extracted from
120 the most recent reanalysis data from ECMWF's (European Centre for Medium-range
121 Weather Forecasts), new land component of the fifth generation of European Reanalysis
122 (ERA5-Land) dataset (daily at 0.1°×0.1° resolution; Munoz-Sabater et al., 2021). We
123 calculated vapor pressure deficit (VPD; kPa) from Tair and RH using Equation 1.

124

$$125 \quad VPD = \left(1 - \frac{RH}{100}\right) \times 0.6107 \times 10^{\frac{7.5 \times T_{air}}{237.3 + T_{air}}} \quad (1)$$

126

127 We re-sampled the Precip, Tair, VPD, and SM values from daily (at 0.1°×0.1°) to 8-day
128 (at 0.05°×0.05°) to match the temporal and spatial resolution of vegetation response
129 dataset (see next section).

130 *Forest canopy response dataset*

131 In order to assess the forest canopy response to drought stress, we used two satellite-
132 based proxies: 1) the structure-based NIRv (near-infrared of vegetation index derived
133 from MODIS (Moderate Resolution Imaging Spectroradiometer)(Equation 2), and 2) the
134 physiological-based reconstructed global OCO-2 solar induced fluorescence (SIF). NIRv
135 was estimated following Badgley et al. (2017) as:

$$136 \quad NIR_V = R_{NIR} \times \frac{R_{NIR} - R_{Red}}{R_{NIR} + R_{Red}} \quad (2)$$

137

138 where, R_{NIR} and R_{Red} are the surface spectral reflectance at near-infrared band (band 2
139 of MODIS) and reflectance at red band (band 1 of MODIS), respectively. We obtained the
140 R_{NIR} and R_{Red} from MODIS MOD09Q1 v6.1 product which provides R_{NIR} and R_{Red} at a 8-
141 day temporal and 500m spatial resolution. The calculated NIRv at 500m resolution was
142 aggregated (by mean) at a 0.05°×0.05° resolution. Solar-induced fluorescence (SIF) is



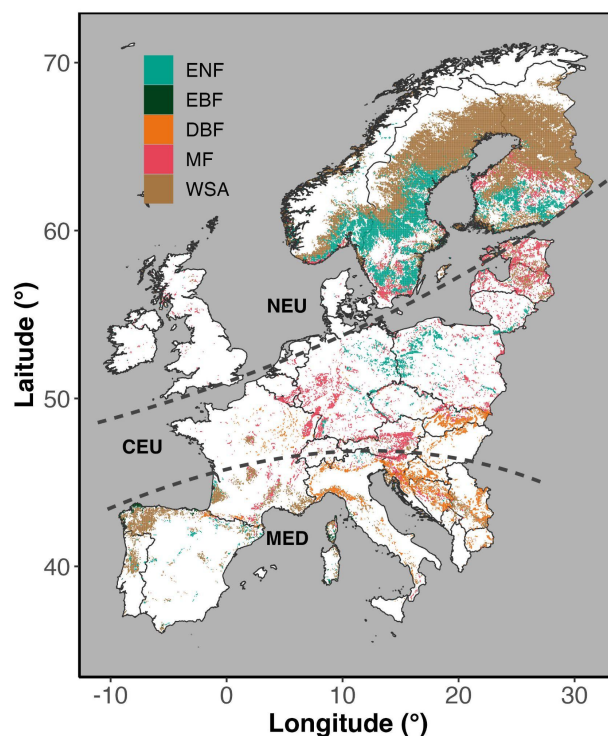
143 linked to vegetation photosynthesis and can be used as a proxy for the ecosystem's gross
144 primary productivity (GPP) (Li et al. 2018; Magney et al. 2019). SIF was available from
145 2000-2022 at 8-day temporal scale with a spatial resolution of $0.05^{\circ} \times 0.05^{\circ}$ (Li and Xiao,
146 2019). SIF signals provide information about physiological response of forest
147 photosynthesis while NIRv (a recently developed vegetation index) signals provide
148 information about the health status of the canopy. NIRv is preferred over NDVI and EVI
149 as it can isolate the vegetated signal, mitigate mixed-pixel issue, and partly address the
150 influences of background brightness and soil contamination (Zhang et al. 2022). The two
151 indices are expected to provide complementary information on vegetation functions.

152 *Land cover dataset*

153 In this study we focused on five different types of forests (and woodlands) across Europe,
154 namely, evergreen needleleaf forest (ENF), evergreen broadleaf forest (EBF), deciduous
155 broadleaf forest (DBF), mixed forest (MF), and woody savannas (WSA). The spatial
156 distribution of the five different forest types across Europe is shown in Figure 1. We used
157 the yearly MODIS land cover product (MCD12C1 version 6.1 at $0.05^{\circ} \times 0.05^{\circ}$ resolution)
158 for the years of 2001, 2006, 2011, 2016 and 2021, to extract total areas covered by each
159 forest type. Only areas that were consistently identified as each forest type in those five
160 years were included in the analysis. This means that only pixels common across the
161 selected five years were selected (Supplementary Fig. 1), and with more than 50% of the
162 $0.05^{\circ} \times 0.05^{\circ}$ pixel area identified as forests (Supplementary Fig. 1). The selected forested
163 area in this study covered an area of 907'875 km² (about 24% of total land area of Europe)
164 (Figure S1). Out of the total area about 23% (206'212 km²) was dominated by ENFs



165 distributed largely across Northern Europe (NEU). Approximately 1% (7'000 km²) of the
166 area was dominated by EBFs, located entirely in Mediterranean Europe (MED), and about
167 10% (92'209 km²) was dominated by DBF which was largely distributed across MED.
168 Approximately 20% (174'934 km²) of the total forested area was dominated by MFs
169 largely dominating Central Europe (CEU), and about 47% (427'529 km²) was dominated
170 by WSA mostly found in NEU (Figure 1).
171



172
173 **Figure 1** Spatial coverage of forests (ENF - evergreen needleleaf forest; EBF - evergreen
174 broadleaf forest; DBF - deciduous broadleaf forest; MF - mixed forest), and woodlands (WSA -
175 woody savannas) across Europe, after selection (see methods). Areas are differentiated into
176 Northern Europe (NEU), Central Europe (CEU), and Mediterranean Europe (MED) following
177 Markonis et al. (2021). The map is based on MODIS land cover product MCD12C1 (version 6.1).

178
179



180 *Statistical data analysis*

181 The focus of our analysis was on the summer months during three extreme years of 2003,
182 2018 and 2022. For this purpose, we subset our meteorological (Precip, Tair, and VPD),
183 soil moisture (SM), and vegetation proxy (NIRv and SIF) datasets for the months of June,
184 July, August (JJA) which comprised of fourteen 8-day periods, for each forested pixel
185 between 2000 and 2022.

186 In order to exclude any impact of the observed greening trend across Europe on the
187 anomalies of vegetation proxies during the extreme years (2003, 2018, 2022), we used
188 detrended summer mean NIRv and SIF. Detrending of summer mean NIRv and SIF from
189 2000-2022 was done pixel-wise based on a simple linear regression model (Buras et al.,
190 2020). We calculated pixel-wise standardized summer anomalies (in terms of z-score,
191 Var_z) for all the variables (Var), i.e., Precip, Tair, VPD, SM, NIRv, and SIF, for each
192 extreme year using Equation 3. Z-scores less than -1 and more than 1 indicate significant
193 negative and significant positive anomalies beyond normal variability. Var_z is calculated
194 as:

195

$$196 \quad Var_z \text{ (unitless)} = \frac{Var - Var_{mean}}{Var_{sd}} \quad (3)$$

197

198 where, Var_{mean} and Var_{sd} are mean and standard deviation of any variable over the 2000-
199 2022 period. Areas were categorized as under drought if $VPD_z > 1$ & $SM_z < -1$, and as
200 normal areas if $-1 < VPD_z < 1$ & $-1 < SM_z < 1$. We used the Pearson correlation coefficient
201 (r) and partial correlation coefficients (Pr) to understand the spatial (across space for each
202 year) and temporal (during each year) correlation of SIF and NIRv anomalies with SM and
203 VPD anomalies (Dang et al., 2022). We calculated the partial correlation coefficient using
204 equations 4-7:

205

$$206 \quad Pr(SIF, SM) = \frac{r(SIF, SM) - r(SIF, VPD) \times r(SM, VPD)}{\sqrt{1 - r(SIF, VPD)^2} - \sqrt{1 - r(SM, VPD)^2}} \quad (4)$$

207

$$208 \quad Pr(SIF, VPD) = \frac{r(SIF, VPD) - r(SIF, SM) \times r(SM, VPD)}{\sqrt{1 - r(SIF, SM)^2} - \sqrt{1 - r(SM, VPD)^2}} \quad (5)$$



209

$$210 \quad Pr(NIRv, SM) = \frac{r(NIRv, SM) - r(NIRv, VPD) \times r(SM, VPD)}{\sqrt{1 - r(NIRv, VPD)^2} - \sqrt{1 - r(SM, VPD)^2}} \quad (6)$$

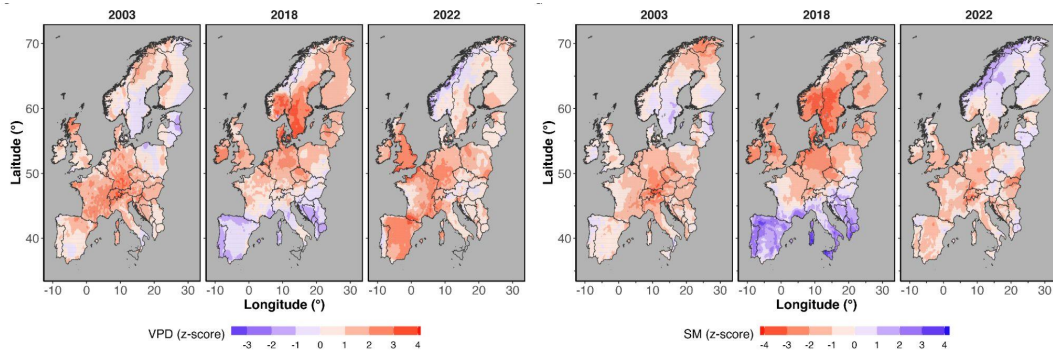
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$$212 \quad Pr(NIRv, VPD) = \frac{r(NIRv, VPD) - r(SIF, SM) \times r(SM, VPD)}{\sqrt{1 - r(NIRv, SM)^2} - \sqrt{1 - r(SM, VPD)^2}} \quad (7)$$

213 Results

214 Severity of the 2022 summer drought compared to 2018 and 2003

215 Figure 2 shows the extent and magnitude of anomalies (z-score) of VPD and top layer (0-
 216 7 cm) soil moisture content during the summer months in 2003, 2018, and 2022 across
 217 the entire region of Europe. In summer 2022, particularly southern regions of Europe
 218 experienced the most pronounced increase in atmospheric (z-score > 1) and soil dryness
 219 (z-score < -1) (Figure 2) while in 2018 we observed the most widespread drought in
 220 northern Europe (Figure 2).



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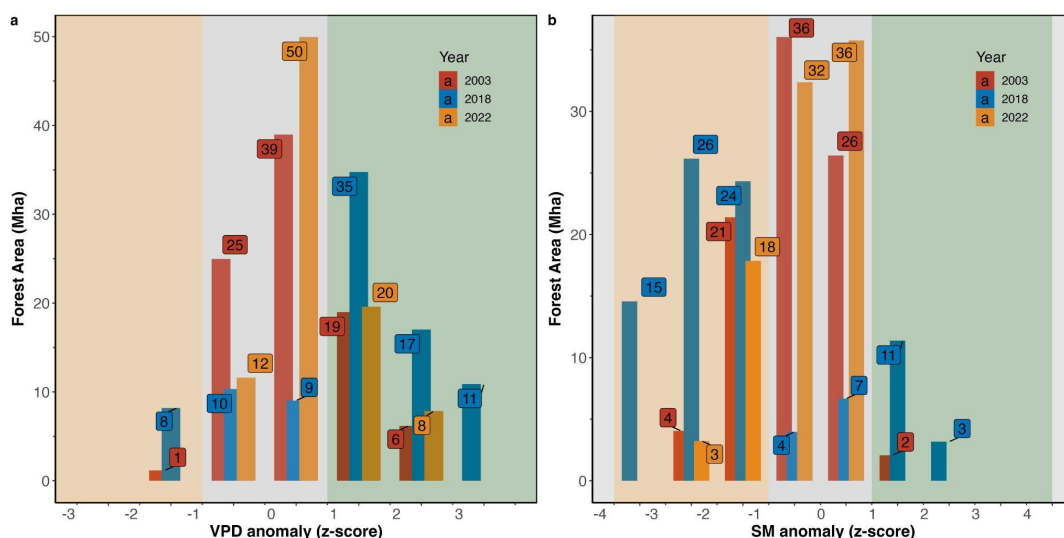
222 **Figure 2** Standardized summer (JJA) anomalies (z-score) of mean vapor pressure deficit (VPD),
 223 and top layer (1-7 cm depth) soil moisture (SM) in 2003, 2018 and 2022, across the region of
 224 Europe.

225

226 Restricted to forested areas, atmospheric and soil drought was 55% and 58% more
 227 extensive in 2018 compared to 2022 (and both years more extensive than in 2003, Figure
 228 3). In 2022, 28 Mha of forested areas in Europe experienced an extremely high VPD (z-
 229 score > 1), while in 2018 63 Mha experienced such extreme conditions. In 2022, 21 Mha



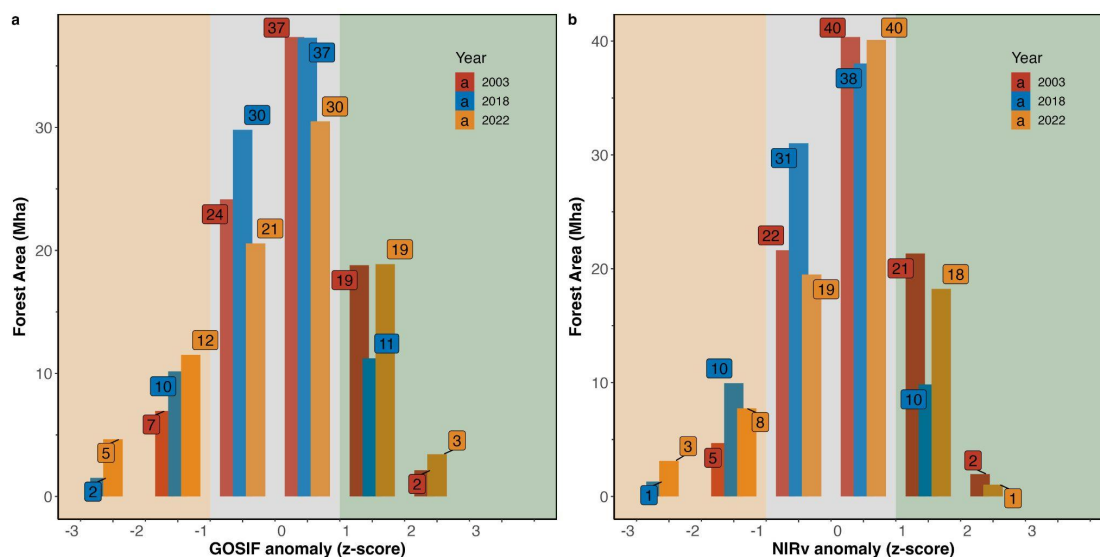
230 of forested areas experienced an extremely low soil moisture content (z-score < -1) while
 231 in 2018, 50 Mha of forests in Europe were affected by such extreme conditions. In 2003
 232 an area of 25 Mha was affected by extremely dry air and a similar area was affected by
 233 extremely dry soil (Figure 3).
 234



235
 236 **Figure 3** Intensity (z-score) and extent (area affected, Mha) of (a) VPD, and (b) SM anomalies
 237 across forested areas. Z-score, values from -1 and 1 are considered normal (within 1 standard
 238 deviation of the mean).
 239

240 *Forest canopy response to the 2022 drought*

241 Compared to 2018, the extremely dry conditions in 2022 led to 30% increase in forested
 242 areas that exhibited declined photosynthesis (17 Mha in 2022 compared to 12 Mha in
 243 2018) (Figure 4). The extent of the canopy browning observed in 2022 was similar to
 244 2018, which in both years was 120% of the extent of observed canopy browning in 2003
 245 (11 Mha compared to 5 Mha observed in 2003) (Figure 4).
 246



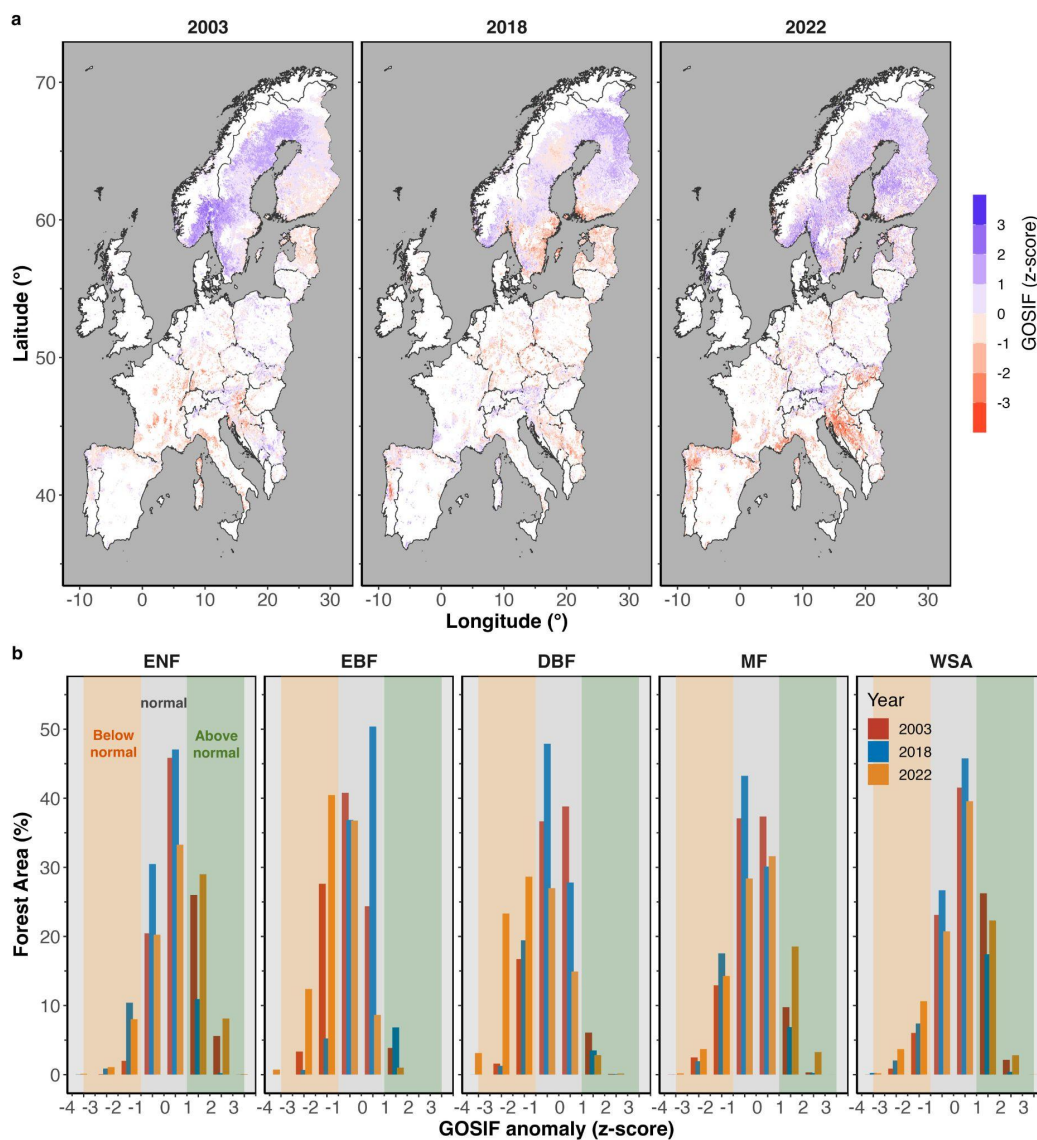
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248

249 **Figure 4** Intensity (z-score) and extent (area affected, Mha) for (a) SIF, and (b) NIRv anomalies
250 across forested areas. Z-score, values from -1 and 1 are considered normal (within 1 standard
251 deviation of the mean).

252

253 Across specific forest types, DBFs showed the largest negative SIF anomaly in 2022 but
254 the ENFs showed a positive SIF anomaly in 2022, both in terms of magnitude and in
255 terms of the spatial extent of negative SIF anomalies (Figure 5). In terms of canopy
256 browning response (NIRv anomalies), the largest negative NIRv anomalies in 2022 were
257 observed in southern Europe (Figure 6). Largest negative NIRv anomalies (indicated by
258 the maximum anomaly) were observed in the DBFs in 2022, fitting the declined SIF
259 signals. The ENFs however showed positive NIRv anomalies in 2022, also both in terms of
260 magnitude and spatial coverage and % of total area affected (Figure 6).



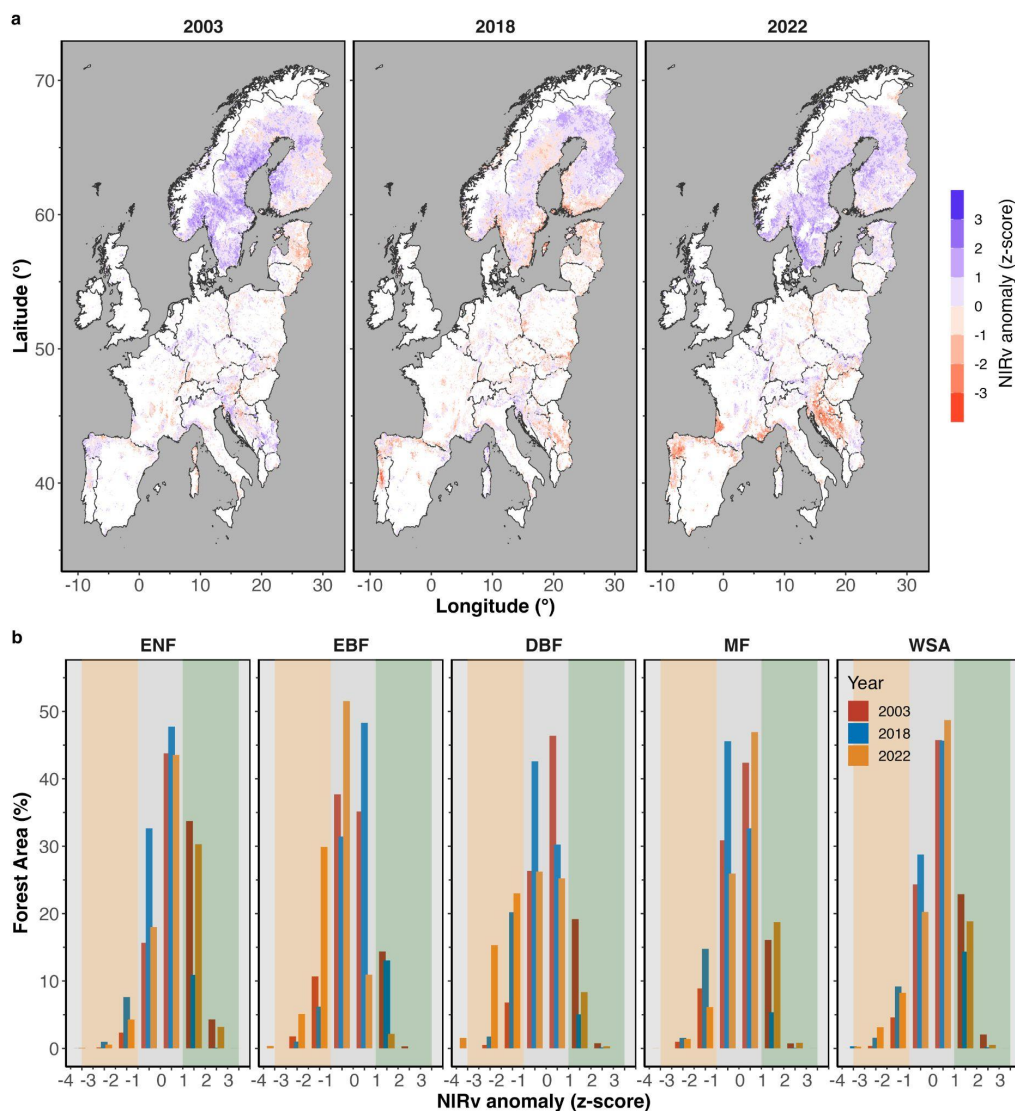
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264

Figure 5 (a) SIF anomaly (in terms of z-score) across Europe, and (b) area coverage (in terms of percentage of total area for each forest type) in 2003, 2018 and 2022.



265

266

267

Figure 6 (a) NIRv anomaly (in terms of z-score) across Europe, and (b) area coverage (in terms of percentage of total area for each forest type) in 2003, 2018 and 2022.

268

269 *Relationship between SIF and NIRv*

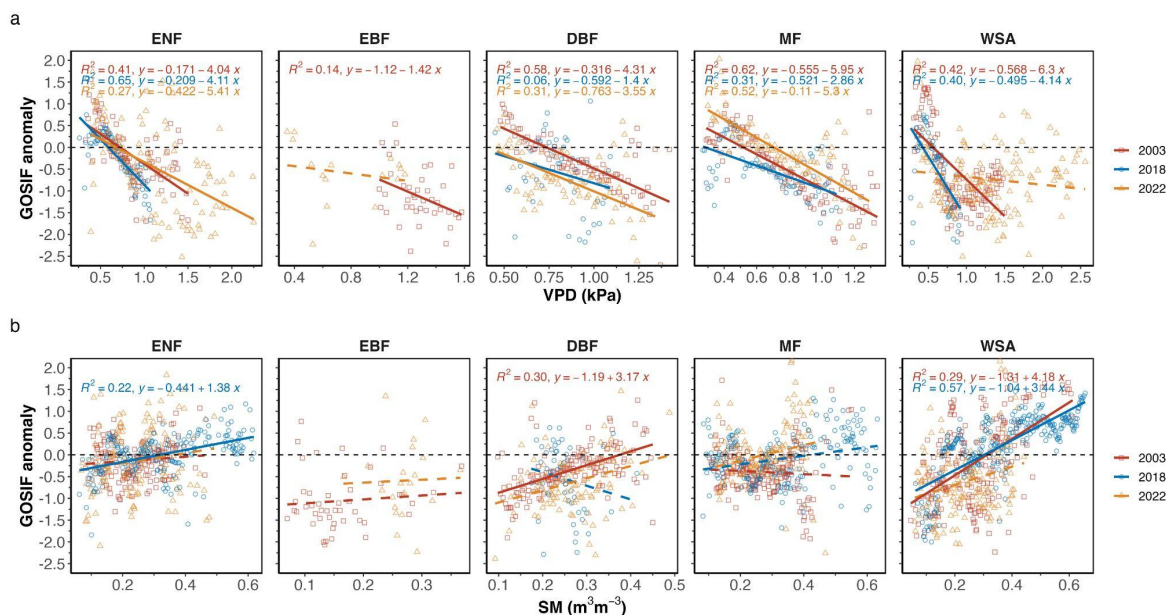
270 In general, the values of NIRv and SIF were highly correlated (Supplementary Figure 1).

271 The anomalies in NIRv and SIF were most correlated across WSAs (mean $r^2 = 0.62$) and

272 least correlated across the ENFs (Supplementary Figure 1). With the increase in VPD



273 positive anomalies (i.e., increased atmospheric dryness), SIF values declined across all
 274 forest types, across all years, except in 2022 in the WSA, and in 2018 and 2022 in EBFs
 275 (Figure 7). With decrease in soil moisture (i.e., increased soil dryness), SIF values also
 276 declined overall ($r^2 = 34$), but not as strongly as with the increase in air dryness ($r^2 = 39$)
 277 (Figure 7). Across different forest types, SIF responded most strongly to VPD anomalies
 278 in the MFs (mean $r^2 = 0.48$), and responded most directly to changes in the soil moisture
 279 in the WSA (Figure 7).

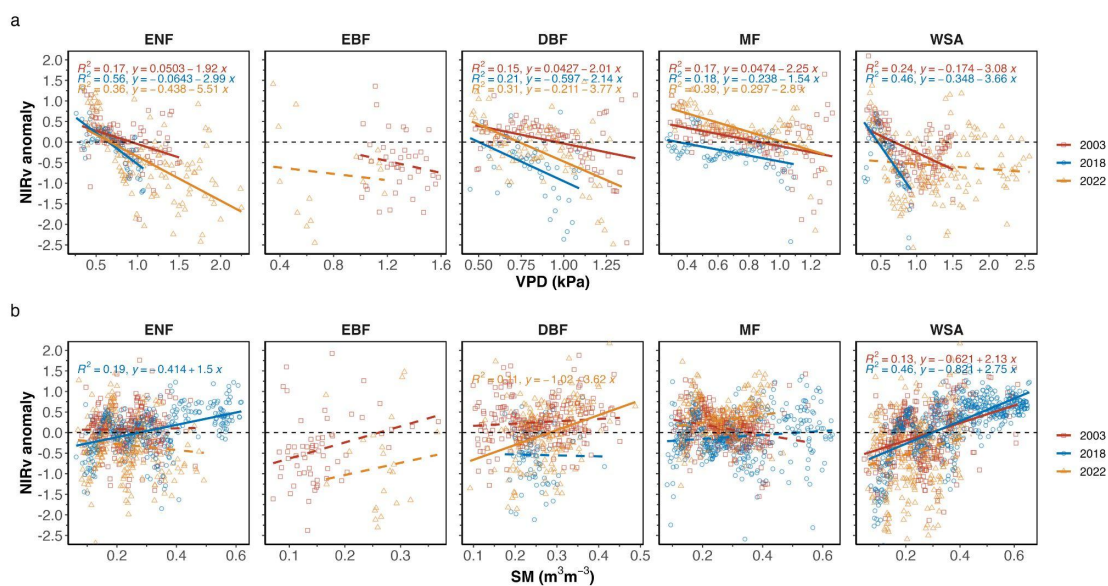


280
 281 **Figure 7** Spatial regression between standardized SIF anomalies with (a) VPD and (b) SM over
 282 the drought areas in summers 2003, 2018 and 2022. Dashed lines mark an insignificant
 283 relationship ($p > 0.05$).

284
 285 Between VPD and SM, in general SIF anomalies were more correlated with VPD than
 286 with SM anomalies, and the decline in VPD correlated well with the larger SIF decline that
 287 we observed in DBFs in 2022 and in ENFs in 2003 (Figure 7). Under general conditions
 288 (regardless of drought), response of SIF to both air dryness and soil moisture anomalies
 289 were larger than the response of NIRv ($r^2 = 0.39$ with SIF, compared to $r^2 = 0.29$ for NIRv)
 290 (Figure 7, 8).

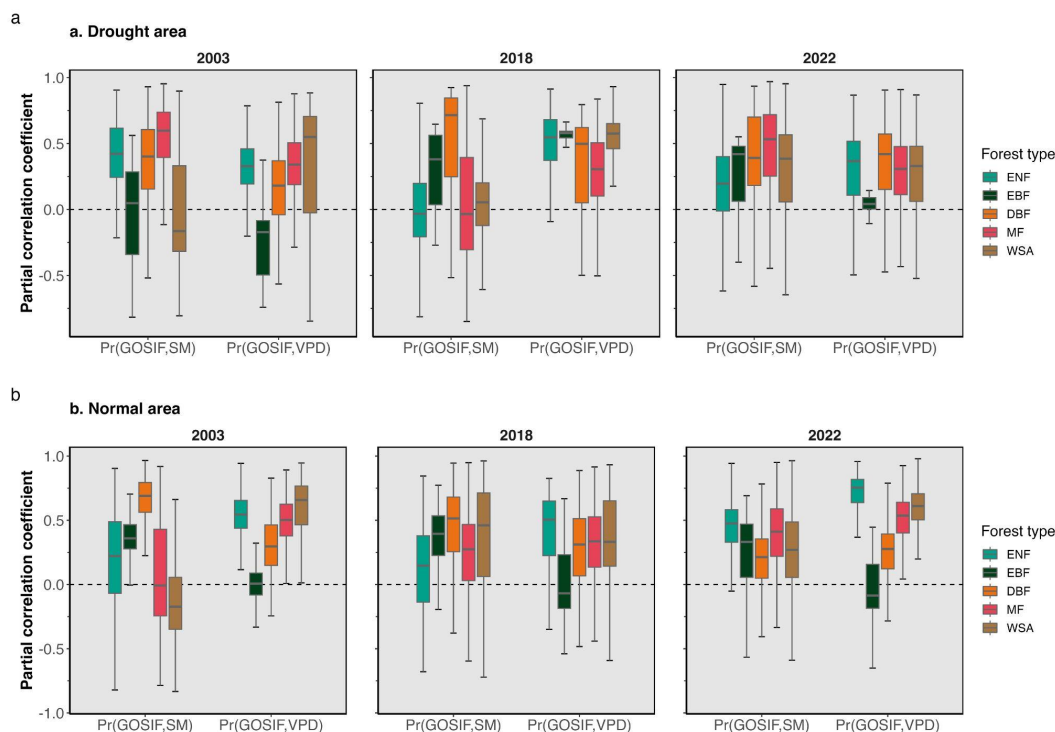


291 The SM and VPD anomalies across all forest types correlated well, but across DBFs the
 292 dryness in the atmosphere and the dryness in the soil were most correlated (Figure 9). In
 293 terms of canopy response to VPD, ENF were the forests that responded most strongly to
 294 changes in the atmospheric dryness (Figure 9).
 295



296
 297 **Figure 8.** Spatial (over all pixels) regression between standardized NIRv anomalies with (a) VPD
 298 and (b) SM over the drought areas and normal areas in 2003, 2018 and 2022.

299
 300



301

302 **Figure 9.** Temporal partial correlation coefficient of SIF with SM and VPD during summer for
303 detected (a) drought areas and (b) normal areas. A similar figure for NIRv is Supplementary Figure
304 2.

305 Discussion

306 *Severity of the 2022 summer drought*

307 While the three selected years (2003, 2018, 2022) are all characterized as “extreme”
308 years, characteristics of the extreme conditions varied largely across the years. In 2003
309 for example, the widespread negative anomalies in soil moisture indicated a significant
310 soil drought, while in 2022 widespread larger positive VPD anomalies, signaled a drier
311 atmosphere (Figure 3). The widespread summer drought in 2022 affected mainly regions
312 of southern Europe, as opposed to the 2003 summer drought that affected central
313 Europe, or the 2018 summer drought that affected central and northern Europe (Figure
314 2) (Bastos et al. 2020). As a result, the extremely dry conditions in 2022 led to an average



315 30% more widespread decline in SIF across forests, compared to 2018, and a 60% more
316 widespread decline compared to 2003 (Figure 4).

317 The above-normal drier conditions during the summer compromised the photosynthetic
318 capacity of plants, and with that the capacity of the ecosystem for carbon uptake from the
319 atmosphere (Peters et al. 2018; van der Woude et al. 2023). Although the atmospheric
320 and soil drought were more extensive and severe (indicated by max observed z-score) in
321 2018 compared to 2022, the negative impact on forests, indicated by declined SIF, was
322 larger in 2022 pointing to a decreased resilience of forests to drought since previous
323 conditions in 2018.

324 *Canopy response to soil versus atmospheric dryness*

325 SIF products prove to be a reliable proxy for vegetation gross productivity, as comparison
326 with ground-based flux measurements show (Shekhar et al. 2022; Pickering et al. 2022).
327 NIRv and SIF signals correspond well and are known to present seasonal patterns in
328 GPP well (Getachew Mengistu et al. 2021). While the strength of their relationship varies
329 across time and space, and with changes in the forest type (Supplementary Figure 1),
330 reductions in SIF signals can be directly linked to reduced photosynthesis. While both SIF
331 and NIRv are good indicators of canopy response to extreme climate, SIF reflects a better
332 effect of short-term changes in the climate (Figure 7).

333 Our analysis showed that across different regions, SIF anomalies corresponded more
334 strongly to increased atmospheric dryness than to increased soil dryness (Figure 7). This
335 fits the notion that for trees, vapor pressure deficit plays a larger role in controlling the SIF
336 signals than soil moisture over shorter time scales (Pickering et al. 2022). Over shorter
337 time frames, soil moisture deficit can be mitigated by various mechanisms within the
338 rooting zone and through plant's access to deeper sources of water, whereas no such
339 buffer exists for the impact of atmospheric dryness on tree canopies. Ground-based
340 observations in forest ecosystems (e.g., based on ecosystem or tree-level
341 measurements) have shown that atmospheric dryness can impose constraints on canopy
342 gas exchange, even when soil moisture is not within a limiting range (Gharun et al. 2014,
343 Fu et al. 2022, Shekhar et al. 2024). These findings emphasize the significance of
344 considering atmospheric dryness in limiting tree photosynthesis during extremely dry



345 conditions, and demonstrate the fast response of a range of canopy types to increased
346 levels of environmental dryness.

347 *Canopy response to drought across different forest types*

348 The spread of drought, as the total sum of areas across z-scores, exhibited different
349 patterns in different years, leading to varied responses of different forest types to the
350 climatic anomalies. Impact of drought on forests can vary largely depending on the forest
351 type, tree species, and factors that are controlled by species composition, and past
352 exposure to extreme conditions (Arthur and Dech 2016; Chen et al. 2022). Our analysis
353 showed that conditions in summer 2022 reduced vegetation functioning across DBFs the
354 most, as it was indicated by declined SIF signals (Figure 5). While deciduous broad-
355 leaved forests were most negatively affected by the extreme conditions in 2022,
356 Evergreen Needle-Leaf Forests (ENF) distributed in northern regions of Europe showed
357 enhanced canopy greening and SIF signals, through benefiting from the episodic warming
358 (Forzieri et al. 2022). The mechanisms to cope with the level of drought stress, vary
359 largely among forest types, and depend on a combination of characteristics that control
360 water loss through the coordination of stomatal regulation, hydraulic architecture, and root
361 characteristics (e.g., rooting perth, root distribution, root morphology) (Gharun et al. 2020;
362 Peters et al. 2023). Stomata of trees exhibit a high sensitivity to VPD fluctuations, causing
363 a reduction in stomatal conductance as VPD increases, which, in turn, limits the exchange
364 of CO₂ with the atmosphere during photosynthesis (Bonal and Guehl in 2011; Li et al.
365 2023). Tree species exhibit varying degrees of sensitivity in their stomatal regulation
366 response to increasing atmospheric dryness (Oren et al. 1999). For instance, ring-porous
367 species tend to maintain robust gas exchange even under dry conditions, in contrast to
368 diffuse-porous species like evergreen needle-leaf forests (ENFs), which adopt a stronger
369 stomatal regulation, reducing stomatal conductance as water availability becomes more
370 limited (Klein 2014). This variance places plants on a spectrum of drought tolerance (Klein
371 2014), representing their specific water relations strategy and leads to different responses
372 of forests within similar climate regions.

373 *Increased frequency of extremes and declined resilience of forests*



374 Higher degree of canopy damage that we observed in 2022, despite less severe
375 conditions compared to the previous extreme year, points towards a lasting impact on
376 forest canopies—a sign of decreased forest resilience in the face of more frequent
377 drought events (Forzieri et al. 2022). The observed decline in forest resilience indicates
378 possible significant implications for vital ecosystem services, including forest capacity for
379 mitigating climate change. Consequently, there is an increasing urgency to consider these
380 trends when formulating robust forest-based mitigation strategies. This is particularly
381 critical as future projections indicate that the frequency and intensity of extreme dryness
382 will continue to increase across Europe by more than 3-fold by the end of the 21st century
383 (Shekhar et al. 2023b). In this context, it becomes increasingly important to investigate
384 the vulnerability of forests to external perturbations, and to base the mitigation of drought
385 legacy effects on management strategies that are tailored to site-specific ecophysiological
386 and environmental factors that control the resilience of forests to drought (McDowell et al.
387 2020; Wang et al. 2023; Shekhar et al. 2024).

388

389 **Conclusion**

390 The severity of the 2022 summer drought, characterized by increased atmospheric
391 dryness, significantly compromised the photosynthetic capacity of trees, leading to
392 widespread declines in vegetation functioning, particularly evident in deciduous broad-
393 leaved forests. Our findings highlight the importance of considering atmospheric dryness
394 as a critical factor influencing canopy responses during extreme climatic events,
395 alongside soil moisture deficit. Despite less severe overall conditions compared to
396 previous extreme years, the observed higher degree of canopy damage in 2022 suggests
397 a declining resilience of forests to drought, raising concerns about the future climate
398 mitigation capacity of forest ecosystems, as projections indicate a continued increase in
399 the frequency and intensity of extreme dryness across Europe.

400

401 **Competing interests**

402 Mana Gharun is a guest editor of the Special Issue and the authors also have no other
403 competing interests to declare

404



405 **Acknowledgements**

406 AS acknowledges funding from the SNF funded project EcoDrive (IZCOZ0_198094).

407



408 References

- 409 Anjileli, H., Huning, L.S., Moftakhari, H. et al. (2021) Extreme heat events heighten soil
410 respiration. *Sci Rep* 11, 6632. <https://doi.org/10.1038/s41598-021-85764-8>
- 411 Arthur CM, Dech JP (2016) Species composition determines resistance to drought in dry
412 forests of the Great Lakes - St. Lawrence forest region of central Ontario. *Journal of Vegetation*
413 *Science* 27, 914-925.
- 414 Badgley G et al. (2017) Canopy near-infrared reflectance and terrestrial photosynthesis. *Sci.*
415 *Adv.* 3, e1602244. DOI:10.1126/sciadv.1602244
- 416 Bastos A et al. (2020) Impacts of extreme summers on European ecosystems: a comparative
417 analysis of 2003, 2010 and 2018. *Phil. Trans. R. Soc. B* 375: 20190507.
418 <http://dx.doi.org/10.1098/rstb.2019.0507>
- 419 Bauke, S. L., Amelung, W., Bol, R., Brandt, L., Brüggemann, N., Kandeler, E., Meyer, N., Or,
420 D., Schnepf, A., Schloter, M., Schulz, S., Siebers, N., von Sperber, C., & Vereecken, H. (2022).
421 Soil water status shapes nutrient cycling in agroecosystems from micrometer to landscape
422 scales. *Journal of Plant Nutrition and Soil Science*, 185, 773–792.
423 <https://doi.org/10.1002/jpln.202200357>
- 424 Bonal, D. & Guehl, J.-M. (2011) Contrasting patterns of leaf water potential and gas exchange
425 responses to drought in seedlings of tropical rainforest species. *Functional Ecology*, 15, 490–
426 496.
- 427 Buras, A., Rammig, A., and Zang, C. S. (2020) Quantifying impacts of the 2018 drought on
428 European ecosystems in comparison to 2003, *Biogeosciences*, 17, 1655–1672,
429 <https://doi.org/10.5194/bg-17-1655-2020>.
- 430 Chen, Y., Vogel, A., Wagg, C. et al. (2022) Drought-exposure history increases
431 complementarity between plant species in response to a subsequent drought. *Nat Commun*
432 13, 3217. <https://doi.org/10.1038/s41467-022-30954-9>
- 433 Choat, B., Brodribb, T.J., Brodersen, C.R. et al. (2018) Triggers of tree mortality under drought.
434 *Nature* 558, 531–539. <https://doi.org/10.1038/s41586-018-0240-x>



- 435 Cornes, R. C., van der Schrier, G., van den Besselaar, E. J. M., & Jones, P. D. (2018). An
436 Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. *Journal of*
437 *Geophysical Research: Atmospheres*, 123(17), 9391–9409.
438 <https://doi.org/10.1029/2017JD028200>
- 439 Dang, C., Shao, Z., Huang, X., Qian, J., Cheng, G., Ding, Q., & Fan, Y. (2022). Assessment of
440 the importance of increasing temperature and decreasing soil moisture on global ecosystem
441 productivity using solar-induced chlorophyll fluorescence. *Global Change Biology*, 28(6),
442 2066–2080. <https://doi.org/10.1111/gcb.16043>
- 443 Drake JE, Tjoelker MG, Vårhammar A, Medlyn BE, Reich PB, Leigh A, Pfautsch S,
444 Blackman CJ, López R, Aspinwall MJ, Crous KY, Duursma RA, Kumarathunge D, De Kauwe
445 MG, Jiang M, Nicotra AB, Tissue DT, Choat B, Atkin OK, Barton CVM (2018) Trees tolerate
446 an extreme heatwave via sustained transpirational cooling and increased leaf thermal
447 tolerance. *Glob Change Biol.* 24: 2390–2402. <https://doi.org/10.1111/gcb.14037>
- 448 Forzieri, G., Dakos, V., McDowell, N.G. et al. (2022) Emerging signals of declining forest
449 resilience under climate change. *Nature* 608, 534–539. [https://doi.org/10.1038/s41586-022-](https://doi.org/10.1038/s41586-022-04959-9)
450 [04959-9](https://doi.org/10.1038/s41586-022-04959-9)
- 451 Fu, Z., Ciais, P., Prentice, I.C. et al. Atmospheric dryness reduces photosynthesis along a large
452 range of soil water deficits. *Nat Commun* 13, 989 (2022). [https://doi.org/10.1038/s41467-022-](https://doi.org/10.1038/s41467-022-28652-7)
453 [28652-7](https://doi.org/10.1038/s41467-022-28652-7)
- 454 Gessler, A., Bottero, A., Marshall, J. and Arend, M. (2020), The way back: recovery of trees
455 from drought and its implication for acclimation. *New Phytol*, 228: 1704-1709.
456 <https://doi.org/10.1111/nph.16703>
- 457 Getachew Mengistu, A., Mengistu Tsidu, G., Koren, G., Kooreman, M. L., Folkert Boersma, K.,
458 Tagesson, T., Ardö, J., Nouvellon, Y., & Peters, W. (2021). Sun-induced fluorescence and
459 near-infrared reflectance of vegetation track the seasonal dynamics of gross primary
460 production over Africa. *Biogeosciences*, 18(9), 2843-2857. [https://doi.org/10.5194/bg-18-2843-](https://doi.org/10.5194/bg-18-2843-2021)
461 [2021](https://doi.org/10.5194/bg-18-2843-2021)



- 462 Gharun M., Vervoort R.W., Turnbull T.L., Adams M.A. (2014) A test of how coupling of
463 vegetation to the atmosphere and climate spatial variation affects water yield modelling in
464 mountainous catchments 514, pp. 202-213. <https://doi.org/10.1016/j.jhydrol.2014.04.037>
- 465 Gharun M., Hörtnagl L., Paul-Limoges E., Ghiasi S., Feigenwinter I., Burri S., Marquardt K.,
466 Etzold S., Zweifel R., Eugster W., Buchmann N (2020) Physiological response of Swiss
467 ecosystems to 2018 drought across plant types and elevation *Phil. Trans. R. Soc.*
468 B3752019052120190521. <http://doi.org/10.1098/rstb.2019.0521>
- 469 Gourlez de la Motte L, Beauclaire Q, Heinesch B, Cuntz M, Foltýnová L, Šigut L, Kowalska N,
470 Manca G, Ballarin IG, Vincke C, Roland M, Ibrom A, Lousteau D, Siebicke L, Neiryink J,
471 Longdoz B. (2020) Non-stomatal processes reduce gross primary productivity in temperate
472 forest ecosystems during severe edaphic drought. *Philos Trans R Soc Lond B Biol Sci.*
473 375(1810):20190527. doi: 10.1098/rstb.2019.0527.
- 474 Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký,
475 M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., van den Hoogen, J., Arriga, N., Brůna, J.,
476 Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P. ... Van Meerbeek, K.
477 (2023). ForestClim—Bioclimatic variables for microclimate temperatures of European forests.
478 *Global Change Biology*, 29, 2886–2892. <https://doi.org/10.1111/gcb.16678>
- 479 Humphrey V, Zscheischler J, Ciais P, Gudmundsson L, Sitch S, Seneviratne SI. (2018)
480 Sensitivity of atmospheric CO₂ growth rate to observed changes in terrestrial water storage.
481 *Nature*, 560 (7720): 628 DOI: 10.1038/s41586-018-0424-4.
- 482 Klein Tank, A. M. G., Wijngaard, J. B., Können, G. P., Böhm, R., Demarée, G., Gocheva, A.,
483 Mileta, M., Pashiardis, S., Hejkrlik, L., Kern-Hansen, C., Heino, R., Bessemoulin, P., Müller-
484 Westermeier, G., Tzanakou, M., Szalai, S., Pálsdóttir, T., Fitzgerald, D., Rubin, S., Capaldo,
485 M., ... Petrovic, P. (2002). Daily dataset of 20th-century surface air temperature and
486 precipitation series for the European Climate Assessment. *International Journal of Climatology*,
487 22(12), 1441–1453. <https://doi.org/10.1002/joc.773>
- 488 Klein, T. (2014), The variability of stomatal sensitivity to leaf water potential across tree species
489 indicates a continuum between isohydric and anisohydric behaviours. *Funct Ecol*, 28: 1313-
490 1320. <https://doi.org/10.1111/1365-2435.12289>



- 491 Li X et al. (2018) Solar-induced chlorophyll fluorescence is strongly correlated with terrestrial
492 photosynthesis for a wide variety of biomes: first global analysis based on OCO-2 and flux
493 tower observations *Glob. Change Biol.* 24 3990–4008.
- 494 Li, X., Xiao, J. (2019) A global, 0.05-degree product of solar-induced chlorophyll fluorescence
495 derived from OCO-2, MODIS, and reanalysis data. *Remote Sensing*, 11, 517;
496 doi:10.3390/rs11050517.
- 497 Li, F., Xiao, J., Chen, J., Ballantyne, A., Jin, K., Li, B., Abraha, M., John, R. (2023) Global water
498 use efficiency saturation due to increased vapor pressure deficit. *Science*, 381, 672-677. DOI:
499 10.1126/science.adf5041.
- 500 Magney T S et al. (2019) Mechanistic evidence for tracking the seasonality of photosynthesis
501 with solar-induced fluorescence *Proc. Natl Acad. Sci. USA* 116 11640–5.
- 502 Marchin, R. M., Backes, D., Ossola, A., Leishman, M. R., Tjoelker, M. G., & Ellsworth, D. S.
503 (2022). Extreme heat increases stomatal conductance and drought-induced mortality risk in
504 vulnerable plant species. *Global Change Biology*, 28, 1133–1146.
505 <https://doi.org/10.1111/gcb.15976>
- 506 Markonis, Y., Kumar, R., Hanel, M., Rakovec, O., Máca, P., AghaKouchak, A., (2021). The rise
507 of compound warm-season droughts in Europe. *Science Advances* 7.
508 <https://doi.org/10.1126/sciadv.abb9668>
- 509 McDowell, N. G. et al. (2020) Pervasive shifts in forest dynamics in a changing world. *Science*
510 368, eaaz9463.
- 511 Müller, L. M., and M. Bahn (2022) Drought legacies and ecosystem responses to subsequent
512 drought. *Global Change Biology* 28:5086–103. doi:10.1111/gcb.16270.
- 513 Muñoz-Sabater, J., Dutra, E., Agustí-Panareda, A., Albergel, C., Arduini, G., Balsamo, G.,
514 Boussetta, S., Choulga, M., Harrigan, S., Hersbach, H., Martens, B., Miralles, D. G., Piles, M.,
515 Rodríguez-Fernández, N. J., Zsoter, E., Buontempo, C., & Thépaut, J. N. (2021). ERA5-Land:
516 A state-of-the-art global reanalysis dataset for land applications. *Earth System Science Data*,
517 13(9), 4349–4383. <https://doi.org/10.5194/essd-13-4349-2021>



- 518 Peters, W., van der Velde, I.R., van Schaik, E. et al. Increased water-use efficiency and
519 reduced CO₂ uptake by plants during droughts at a continental scale. *Nature Geosci* 11, 744–
520 748 (2018). <https://doi.org/10.1038/s41561-018-0212-7>
- 521 Peters, R.L., Steppe, K., Pappas, C., Zweifel, R., Babst, F., Dietrich, L., von Arx, G., Poyatos,
522 R., Fonti, M., Fonti, P., Grossiord, C., Gharun, M., Buchmann, N., Steger, D.N. and Kahmen,
523 A. (2023), Daytime stomatal regulation in mature temperate trees prioritizes stem rehydration
524 at night. *New Phytol*, 239: 533-546. <https://doi.org/10.1111/nph.18964>
- 525 Pickering, M., Cescatti, A., and Duveiller, G. (2022) Sun-induced fluorescence as a proxy for
526 primary productivity across vegetation types and climates, *Biogeosciences*, 19, 4833–4864,
527 <https://doi.org/10.5194/bg-19-4833-2022>.
- 528 Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N. and Schäfer, K.V.R.
529 (1999), Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to
530 vapour pressure deficit. *Plant, Cell & Environment*, 22: 1515-1526.
531 <https://doi.org/10.1046/j.1365-3040.1999.00513.x>
- 532 Röthlisberger, M., Papritz, L. (2023). Quantifying the physical processes leading to
533 atmospheric hot extremes at a global scale. *Nature Geosci.* 16(3), 210-216.
534 [doi:10.1038/s41561-023-01126-1](https://doi.org/10.1038/s41561-023-01126-1).
- 535 Seidl, R., Thom, D., Kautz, M. et al. Forest disturbances under climate change. *Nature Clim*
536 *Change* 7, 395–402 (2017). <https://doi.org/10.1038/nclimate3303>
- 537 Seneviratne, S. I., Zhang, X., Adnan, M., Badi, W., Dereczynski, C., Di Luca, A., Ghosh, S.,
538 Iskandar, I., Kossin, J., Lewis, S., Otto, F., Pinto, I., Satoh, M., Vicente-Serrano, S. M., Wehner,
539 M., and Zhou, B. (2021) Weather and Climate Extreme Events in a Changing Climate, in:
540 *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the*
541 *Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by:
542 Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen,
543 Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock,
544 T. K., Waterfield, T., Yelekçi, O., Yu, R., and Zhou, B., Cambridge University Press, Cambridge,
545 United Kingdom and New York, NY, USA, 1513–1766,
546 <https://doi.org/10.1017/9781009157896.013>.



- 547 Shekhar, A., Hörtnagl, L., Buchmann, N., & Gharun, M. (2023a). Long-term changes in forest
548 response to extreme atmospheric dryness. *Global Change Biology*, 29, 5379–5396.
549 <https://doi.org/10.1111/gcb.16846>
- 550 Shekhar A, Hörtnagl L, Paul-Limoges E, Etzold S, Zweifel R, Buchmann N, Gharun M (2024)
551 Contrasting impact of extreme soil and atmospheric dryness on the functioning of trees and
552 forests. *Science of the Total Environment* 916, 169931.
553 <https://doi.org/10.1016/j.scitotenv.2024.169931>
- 554 Shekhar A, Buchmann N and Gharun M (2022) How well do recently reconstructed solar-induced
555 fluorescence datasets model gross primary productivity? *Remote Sens. Environ.* 283, 113282
- 556 Shekhar A, Humphrey V, Buchmann N, Gharun M (2023b). More than three-fold increase of
557 extreme dryness across Europe by end of 21st century. [https://doi.org/10.21203/rs.3.rs-](https://doi.org/10.21203/rs.3.rs-3143908/v2)
558 [3143908/v2](https://doi.org/10.21203/rs.3.rs-3143908/v2) (under review in *Weather and Climate Extremes*)
- 559 Tripathy, K. P., & Mishra, A. K. (2023) How unusual is the 2022 European compound drought
560 and heatwave event? *Geophysical Research Letters*, 50, e2023GL105453.
561 <https://doi.org/10.1029/2023GL105453>
- 562 van der Woude, A.M., Peters, W., Joetzjer, E. *et al.* Temperature extremes of 2022 reduced
563 carbon uptake by forests in Europe. *Nat Commun* 14, 6218 (2023).
564 <https://doi.org/10.1038/s41467-023-41851-0>
- 565 van der Molen MK, Dolman AJ, Ciais P et al (2011) Drought and ecosystem carbon cycling.
566 *Agric for Meteorol.* 151(7):765–773. <https://doi.org/10.1016/j.agrformet.2011.01.018>
- 567 Zhang J, Xiao J, Tong X, Zhang J, Meng P, Li J, Liu P, Yu P (2022) NIRv and SIF better
568 estimate phenology than NDVI and EVI: Effects of spring and autumn phenology on ecosystem
569 production of planted forests. *Agricultural and Forest Meteorology* 315, 108819
- 570 Zhou, S., Yu, B. and Zhang, Y. (2023). Global concurrent climate extremes exacerbated by
571 anthropogenic climate change. *Sci. Adv.* 9(10), p.eabo1638. doi:10.1126/sciadv.abo1638.
- 572 Wang B, Chen T, Xu G, Wu G, Liu G (2023) Management can mitigate drought legacy effects
573 on the growth of a moisture-sensitive conifer tree species. *Forest Ecology and Management*
574 544, 121196. <https://doi.org/10.1016/j.foreco.2023.121196>